and instead of gun-cotton, a lower nitrate of cellulose was used. The great factory at Gretna, also built by Mr. Quinan, manufactured R.D.B. cordite exclusively, and this soon became the only propellant made in this country for the Land Service. It was produced both by Government and by private firms in enormous quantities.

The need for ether and alcohol for this propellant led to the restrictions imposed on alcohol.

The recovery of the new solvent presented new problems, and investigations on these were undertaken, which have increased our knowledge of the principles underlying the absorption of vapours.

As difficulties arose in the gelatinisation of the special nitrocellulose required for this powder, the Department continued its studies on the viscosity of cellulose and nitrocellulose with important results, which formed the groundwork of the procedure adopted in supply for obtaining uniformity in the cotton used in the nitration, and a diminished usage of solvent in the incorporation.

Other Explosives.—Many other explosives for special naval and land purposes were put forward by the Department and adopted by the Service after their properties had undergone investigation.

Design of Ammunition.—A feature of the work is the close connection between mechanisms connected with ammunition and the utilisation in them of explosives the properties of which have been found specially suitable. The Department was fortunate in the success which has attended its percussion fuse (No. 106), which played such an important part in the war.

Pyrotechnics.—New demands occasioned by the war led to the study of compositions for pyrotechnic and incendiary purposes and to chemical investigations on the compatibility of the ingredients used. Many new compositions were devised and adopted for signals, stars, and incendiary shell.

Study of the Theory of Explosives.—The study of the chemical constitution of nitro-compounds has been referred to; but a large amount of information the usefulness of which has been reflected on Service requirements has accrued from the development of systematic work on such subjects as the calorimetry of explosives, for which new methods and apparatus have been devised, their sensitiveness, their rates of decomposition and of detonation, and the pressure of the blow they develop. The last was an extension of the work of the late Prof. B. Hopkinson, and has been fruitful in advancing knowledge of theory as well as in providing instruments for quantitative registration of the effects of explosives contained in Service components.

General.—The high quality and efficiency of our ammunition, in spite of shortage and the need for providing substitutes, have been obtained as a result of the continuous application of chemical and physical research. The research initiated and carried out provided in numerous cases methods for the production of explosives, and demonstrated the conditions for their safe employment; principles of fundamental importance were discovered which were utilised in the designing of ammunition; causes of failure at early stages were discovered, thus avoiding unsatisfactory issues of material; and substitutes and alternatives, without which some of our great war manufactures could not have been carried on, were sought and discovered.

(*To be continued.*)

The Earliest Known Land Flora.[1]

By Prof. F. O. Bower, F.R.S.

II.

COMPARISON of these four fossil species from Rhynie with other fossils already known from the early Devonian period shows that a very homogeneous flora existed at that time, consisting chiefly of leafless and rootless land-living plants. These and other characters, such as their large, distal, sometimes solitary, and often forked sporangia, stamp these plants as exceptionally primitive. Among living plants the nearest of kin to them are clearly the Psilotaceæ, a family which has long presented a problem in morphology and classification. It comprises two living genera, Psilotum and Tmesipteris. Both genera are rootless. Their imperfect morphological differentiation is shown by the fact that botanists are not yet agreed whether their lateral appendages are to be held as truly foliar or not. Psilotum is native throughout the tropics, and is represented by two well-marked species. The commonest, *P. triquetrum,* has upright and shrubby aerial shoots, with radial construction and frequent bifurcations. These spring from leafless underground rhizomes, profusely bifurcated. They are covered with rhizoids, and contain a mycorhizic fungus. On the lower part of the aerial shoots simple spine-like leaves are borne, but towards the distal ends these are replaced by forked spurs, between the prongs of which a synangium, usually with three loculi, is seated. The aerial shoot is traversed by a vascular strand consisting of xylem in the form of a hollow many-rayed star, with sclerotic core, and branch-strands run out to the appendages. The whole is covered by epidermis with stomata, and the cortex provides the photosynthetic tissue. Tmesipteris is represented by only one species, limited to Australasia. It grows usually among the massed roots that cover the stems of tree-ferns, but sometimes upon the ground. Its general form is like

[1] Discourse delivered at the Royal Institution on Friday, April 30 Continued from p 684.

that of Psilotum, but the underground rhizomes are longer and the appendages larger, while only two loculi are usually present in each synangium. Clearly the form and vascular structure of these plants are generally like those of the Rhynie flora.

Until quite recently the Psilotaceæ remained the only living Pteridophytes of which the life-cycle was still incompletely known. In all the other groups the regular alternation of two generations had been demonstrated; one is the prothallus, which is sexual, and the other the established plant, which is non-sexual. In the Psilotaceæ also the plant as above described is the non-sexual generation, but hitherto the form or even the existence of the sexual generation remained problematical. Since 1914 the prothalli of both genera of the Psilotaceæ have been discovered, and their structure has been demonstrated by Darnell-Smith, Lawson, and Holloway; and so the very last of these life-histories has now been completed. It turns out that the prothallus of the Psilotaceæ is similar in its general characters to those of other archaic Pteridophytes, being colourless, and living in humus by means of fungal nourishment. In fact, these plants conform in their life-cycle to what is seen in the Lycopods and in the primitive Ferns. Analogy with the living Psilotaceæ makes it highly probable that these early Devonian plants also showed alternation. Though this has not been demonstrated for them, their preservation is so perfect that even the delicate prothallus may yet be revealed as the reward of further search.

The interest of the recent work on the modern Psilotaceæ centres not so much in the details of the prothallus as in their embryology. It has been shown by Holloway that the embryo of Tmesipteris is rootless from the first. This suggests that the rootlessness is primitive, and not the result of reduction. Since the Devonian plants were rootless also, it seems probable that this state was characteristic of such early plants of the land. Further, the existence of Sporogonites, and the very moss-like structure of its sporangium, together with its similarity to the sporangia of Rhynia and Hornea, seem to link up the latter naturally with the Bryophytes, which are also rootless. In fact, we see before us a flora of rootless plants, which raises afresh the question of the first establishment of the neutral generation as an independent, soil-growing organism. It originates in every case within the tissue of the sexual plant, and is at first dependent upon it. This condition is seen in the embryo of Tmesipteris, with details not unlike those of the Anthoceroteæ. How, then, did it first establish itself independently upon the soil?

This question was first raised long ago by Dr. Treub, the brilliant director of the Botanic Gardens at Buitenzorg. He suggested that in the evolution of land-living plants a rootless phase would naturally precede the full establishment of the sporophyte in the soil. He saw this reflected in the embryonic state of certain Lycopods, where a parenchymatous tuber precedes the establishment of the rooted plant. It is attached to the soil by rhizoids, and contains a mycorhizic fungus. This tuber Treub styled the "protocorm." He regarded it as a general precursor of the established leafy plant in descent. During the war new examples of this protocorm-stage were described by Holloway, which show the condition in its most pronounced form. In *Lycopodium laterale* it constitutes the whole plant-body for the first season. It bears numerous protophylls, and may even branch, and reproduce itself vegetatively. It is only later that the leafy shoot and lastly the root are formed. The fact that Hornea shows a similar tuberous swelling at the base of the rootless plant, and retains it even in the adult state, brings the added interest that a permanent protocorm figures in the earliest known land flora. Its antiquity is thus undoubted. But the Devonian plants do not all show it in a distended form. The tuberous swelling is not conspicuous in Rhynia or in Asteroxylon, and it is significant that in the living Tmesipteris the rhizome is cylindrical. These facts indicate that the distended protocorm is neither an obligatory nor a constant feature.

It will not be necessary to do more than refer briefly to the controversy whether the appendages of the Psilotaceæ are truly leaves or branches. The fact suffices that the question has been in debate, and that similar questions arise in relation to these fossils of the Devonian period. In them it is impossible to assign the name "leaf" to any definite part in the full sense in which it is used in the higher vascular plants. The difficulties of their morphological analysis and their rootlessness are in themselves evidence of the primitive state of these fossils. We are, in fact, in the presence of what evolutionists call "synthetic types"—that is, such as link together groups which have diverged. The early Devonian plants and the Psilotaceæ show us just those forms which might have been anticipated as a consequence of comparative study, and some of their characters were actually forecast by Dr. Treub.

Though it may be difficult to place the parts of these synthetic types in the categories of stem, leaf, and root, as those terms are applied to more advanced forms, still they will serve to illuminate the probable origin of these parts. The rhizomes of Asteroxylon suggest an origin of roots from branched, leafless rhizomes. Its "leaves" suggest a relation with the leaves of Lycopods; but its most significant feature is the branch-system ascribed to Asteroxylon, bearing the distal sporangia, which is so like that already described for the enigmatical Carboniferous fossil Stauropteris. This comparison has already been pointed out by Kidston and Lang. On the other hand, approaching the question from the side of the living Ferns, I indicated in 1917 that "the distal and marginal position of a sorus, often monangial, is prevalent among primitive Ferns, and that more complex sori are referable in origin to it." Comparison of the distal sporangia of the Psilophytales with those of Stauropteris, Botryopteris, the Ophioglossaceæ, Osmunda, and the Schizæaceæ, gives a sequence which sketches in broad lines, though not monophyletically, a probable origin of marginal sporangia for the Ferns. It is accompanied by reduction of size and spore-number in the later and derivative types, which is continued on to the most advanced of living Ferns. A reduction of the distal branchlets to a single plane, and the webbing of them laterally together, would give a type of sporophyll and fructification known in certain primitive Ferns. But if this were the real course of their evolution, the sporophyll so constructed would be a different thing from the "leaves" seen in Asteroxylon. This was the vision of the prophetic Lignier, who has not lived to see his ideas tested by these new discoveries. But such comparisons still leave in doubt the origin of the axis in fern-like types. It is not clear yet how near the truth for them my suggestion of 1884 may be: that "the stem and leaf would have originated simultaneously by differentiation of a uniform branch-system into members of two categories." Nevertheless, the important new fact, which now gives reality to this theory, is that a uniform branch-system has been shown to have existed in these early vascular plants. A sympodial development of it, after the manner shown in the leaves of living Ferns, would provide at least one type of foliar appendage, which would bear a relation to the axis similar to that of the pinnæ to the phyllopodium or Pachis of the leaf.[2]

On the other hand, comparison of the Bryophytes will leave little doubt that the sporangium of the Psilophytales and the sporogonium are kindred structures. If this be so, then we shall see linked together by comparison with these new fossils, not only the sporogonia of Bryophytes and the sporangia of Ferns, but even the pollen-sacs and ovules of Flowering Plants. Long ago it was remarked that the widest gap in the sequence of plants was that between the Bryophytes and the Pteridophytes. It is within this gap that the newly discovered fossils take their natural place, acting as synthetic links, and drawing together more closely the whole sequence of land-living, sporangium-bearing plants. We still await with interest the considered comparisons of the authors of these notable memoirs, though they have already pointed out several fertile lines. But those who have been deeply engaged in comparative morphology may be excused for stating how these new facts strike them. Clearly the morphology of land-living plants is again in the melting-pot. It will emerge strengthened by new and positive facts, and refined by comparisons which can now be based upon solid data, and less than before on mere surmise.

The new facts are thus seen to link the Bryophytes and the Pteridophytes more closely together than ever before. It may be that these two great phyla of land-living plants have themselves diverged from some common source still unknown. But that source is reflected more nearly in these early Devonian plants than in any other known forms. If that be so, whence may these still more primitive plants have sprung? The view has always been entertained that the Algæ preceded land-living plants. For long the fresh-water green Algæ were believed to have provided the source. Latterly from the Continent, but notably also here at home, at the instance of Lang and of Church, the belief has swung round towards marine forms. Highly specialised Algæ flourish on every rocky shore. Some of these show alternation. All are rootless. Some have a differentiation of their branch-system which prefigures the relation of leaf and axis. Not a few of the Red Seaweeds have spore-tetrads borne internally, and located in the ends of specialised branches called stichidia. These are not altogether unlike sporogonia, or the large sporangia of the early Devonian plants. We may well regard it as improbable that any direct transition of such specialised types to a land-habit took place, though this has been hinted at more than once. But at least corresponding features of external differentiation and of spore-production are present in both. Homoplasy may be the real explanation of the likeness, but still the similarity exists.

From what has been said it is clear that during the years of war plant morphology entered upon a new phase. The problems of origin of root and axis and leaf and sporangium have been propounded afresh in terms of the new discoveries. The day is past of that vague surmise on these points which bulked so largely in the discussions of recent decades. It was the paucity of facts that kept opinion in suspense, hovering between rival arguments rather than settling on assured data. Looking back upon the history of that branch of botanical science which is called comparative morphology, there is only one period that can rival the years from 1913 to 1920 in point of positive advance. It is the period which led up to the great generalisations of Hofmeister sixty years ago. In the glories of that work Britain had no direct share, though it was carried out at the very time when Lyell, Darwin, Wallace, Hooker, and Huxley were laying the theoretical foundations which gave their real significance to the discoveries then made by Hofmeister. In the words of Sachs: "When Darwin's theory was given to the world—the theory of Descent had only to accept what genetic morphology had already brought to view." Science, it is true, is cosmopolitan, and should always be held as such. But still we in Britain may feel a legitimate satisfaction that in these recent discoveries, which have transformed the problems of morphology, the material, the observations, and the arguments based upon them are mainly of British origin. The channel of publication of the results, so largely derived by Scottish workers from Scottish material, has naturally been the Transactions of the Royal Society of Edinburgh.

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[2] Phil. Trans., 1884, p. 565.